DISTRIBUTIONAL PATTERNS OF MAMMALS IN UTAH

David M. Armstrong[1]

Abstract.— Based on a synthesis of recent work on distribution of mammals in Utah, the hierarchy of ecogeographic distributional units proposed by Durrant (1952) is reevaluated by numerical methods. Areographic faunal elements, distinguished on the basis of shapes of distributional ranges in North America, are identified. Relationships are shown between ecogeographic faunal units and areographic faunal elements, and their historical implications are discussed.

Biogeography seeks to describe patterns in the landscape and to understand their evolution. Utah provides a study area of considerable interest to the zoogeographer interested in faunal movements and effects of corridors, barriers, and isolation. The state is large (nearly 85,000 sq mi or 220,000 km^2) and includes a wide range of ecological conditions, from hot desert to alpine tundra. Mean elevation is roughly 6100 ft (1860 m) and the range of relief is from about 2000 ft (610 m where Beaverdam Wash leaves the state in the southwest) to nearly 13,500 ft (4115 m at the summit of Kings Peak in the Uinta Mountains). A north-south "archipelago" of mountains and high plateaus divides Utah roughly in half. The eastern part is drained by the Colorado River and its tributaries, which have carved horizontal sedimentary formations into an intricate landscape of basins and canyons. West of the central highlands lies the Great Basin, a complex area of minor mountain ranges and internal drainage, dominated by the vast bed of Pleistocene Lake Bonneville.

The only previous zoogeographic analysis of mammals of Utah is that of Durrant (1952), who distinguished "faunal areas" in the state. These were ecogeographic units, roughly comparable to the biotic provinces of Dice (1943). Faunal areas were recognized subjectively, by the coincidence between mammalian distributions and physiographic units. Durrant (1952: 480) pointed out that faunal areas tended to be centers of differentiation for subspecies. Kelson (1951) discussed the influence of the Colorado River and its major tributaries on differentiation and distribution of rodents, refining Durrant's work on faunal areas. Marshall (1940) studied ecological biogeography of mammals on islands in the Great Salt Lake. Lee (1960) investigated the montane mammals of several mountain ranges in southeastern Utah in an effort to understand faunal relationships among the highland faunas and the effects of Pleistocene climatic change on the patterns observed. Brown (1971, in press) studied montane mammals of Utah as an example of insular biogeography. Armstrong (1973) discussed zoogeographic relationships of mammals in Canyonlands National Park, which lies astride the confluence of the Colorado and Green rivers. This work in southeastern Utah suggested some intriguing local patterns of ecological and historical biogeography, but the existing literature was inadequate to place the area in a broader context. The present paper is meant as a partial answer to this need. Its purpose is to refine ecogeographic analyses of previous authors and to provide an areographic analysis of the mammals of Utah.

Methods

Analyses of range limits in Utah were based on maps of 92 species. Seventeen species range essentially statewide in suitable

[1]Department of Integrated Studies and University Museum, University of Colorado, Boulder, Colorado 80309.

habitat and hence were not mapped: *Myotis lucifugus*, *Myotis volans*, *Myotis evotis*, *Myotis leibii*, *Lasionycteris noctovagans*, *Eptesicus fuscus*, *Lasiurus cinereus*, *Plecotus townsendii*, *Peromyscus maniculatus*, *Erethizon dorsatum*, *Canis latrans*, *Bassariscus astutus*, *Mustela frenata*, *Taxidea taxus*, *Mephitis mephitis*, *Spilogale putorius*, and *Lynx rufus*. (These species are included in analyses of faunal areas.) Twelve species are known from too few localities to allow their ranges in Utah to be outlined with any confidence: *Sorex merriami*, *Sorex nanus*, *Notiosorex crawfordi*, *Myotis velifer*, *Euderma maculatum*, *Idionycteris phyllotis*, *Tadarida macrotis*, *Ondatra zibethicus*, *Procyon lotor*, *Martes pennanti*, *Lutra canadensis*, *Odocoileus virginianus*. Three species (*Canis lupus*, *Ursus arctos*, and *Bison bison*) have been extirpated in Utah over the last 125 years; limits of their former ranges are unknown. In addition, the natural ranges of *Antilocapra americana* and *Ovis canadensis* have been altered to an unknown extent since the advent of European civilization in Utah.

Range maps for mammals in Utah generally were based on those published by Durrant (1952) and refined using distributional records from the following more recent papers: Anderson 1955, 1959, Armstrong 1972b, 1974, Behle and Hansen 1951, Benson 1954, Black 1970, Brown 1971, in press, Dearden and Lee 1955, Durrant and Hansen 1954, Durrant and Newey 1953, Durrant and Lee 1955, 1956, Durrant, Lee, and Hansen 1955, Durrant and Dean 1959, 1960, Easterla 1965, 1966, Egoscue 1961, 1966, Egoscue and Lewis 1968, Hansen 1953, Harris 1974, Hayward and Killpack 1956, 1958, Hennings and Hoffmann, in press, Genoways and Jones 1967, Keegan 1953, Killpack 1955, Krutsch and Heppenstall 1955, Lee 1960, Lee and Durrant 1960, Lowery and Egoscue 1968, Miller and Kellogg 1955, Musser and Durrant 1960, Nichols et al. 1975, Poché 1975, Poché and Bailie 1974, Poché and Ruffner 1975, Rasmussen and Chamberlain 1959, Shippee and Egoscue 1958, Stock 1970, Thaeler 1972, Wauer 1966, White 1953, Wood 1958. An attempt was made to make range maps at least roughly comparable in their level of resolution. As a check on the redrafted range maps, range limits in Utah were compared to those reported in adjacent states of Idaho (Davis 1939), Nevada (Hall 1946), Arizona (Cockrum 1960), Wyoming (Long 1965), Colorado (Armstrong 1972a), and New Mexico (Findley et al. 1975) and refined where appropriate.

Maps of continental ranges were based on those in Hall and Kelson (1959) with limits in Utah and adjacent states refined on the basis of more recent publications (Cockrum 1960, Long 1965, Armstrong 1972a, Findley et al. 1975) and maps of ranges in Utah prepared for the present paper.

Nine species have been documented in Utah since Durrant's (1952) checklist was published: *Sorex cinereus* (Durrant and Newey 1953), *Sorex nanus* (Durrant and Lee 1955), *Notiosorex crawfordi* (Wauer 1966), *Myotis thysanodes* (Krutsch and Heppenstall 1955), *Idionycteris phyllotis* (Black 1970), *Spermophilus richardsonii* (Hansen 1953), *Perognathus penicillatus* (Stock 1970), *Perognathus fasciatus* (Hayward and Killpack 1956), and *Odocoileus virginianus* (Miller and Kellogg 1955). Two other kinds, *Eutamias umbrinus* (White 1953) and *Thomomys idahoensis* (Thaeler 1972) have been accorded specific status. This brings to 126 the total number of species of recent mammals known from Utah. Most of these species were included by Sparks (1974) in a recent popularized checklist of the mammals of the state. Nomenclature in this paper follows Jones et al. (1975) and Hennings and Hoffmann (in press).

Work on mammals of Canyonlands National Park, of which the present study is a by-product, has been supported by the Society of the Sigma Xi, the Penrose Fund of the American Philosophical Society, the Council on Research and Creative Work of the University of Colorado, and the Canyonlands Natural History Association. I thank Dr. G. L. Kirkland, Jr., for helpful comments on an earlier draft of this paper. The paper is dedicated to the memory of

Stephen D. Durrant, late dean of mammalogists of the Intermountain West.

Results and Discussion

Distributional limits of mammalian species form complex but recurring patterns. These patterns may be described at various levels of resolution and by various means. In a local area, for example, one might be interested in the pattern of habitat requirements of a single species' population, in recurring communities of organisms, or in distribution along altitudinal or other gradients. On a broader scale, concern might be with distribution of species through ecological community types, with ecogeographic units (like the biotic provinces of Dice, 1943) that summarize regional ecological pattern, or with the shapes of species' ranges (areographic analysis). Emphasis here is on ecogeographic and areographic analysis, and the relationships between them. Ecogeographic description summarizes broad environmental patterns; areographic analysis may provide historical clues to the evolution of regional faunas (Armstrong 1972a).

Ecogeographic Considerations.— J. A. Allen (1892) pioneered ecogeographic studies of North American mammals, and Kendeigh (1954) reviewed subsequent work. Dice (1943) developed the concept of the Biotic Province to describe coherent units of regional landscape. Hagmeier and Stults (1964) and Hagmeier (1966) derived "mammal provinces" in North America by numerical methods, based on range maps in Hall and Kelson (1959). Hagmeier (1966) included parts of Utah in six mammal provinces, arranged in his hierarchy of ecogeographic units as follows:

I. Coniferan Subregion
  A. Mountain Superprovince
    1. Coloradan Province
II. Sonoran Subregion
  A. Navajo Superprovince
    1. Navajonian Province
    2. Uintian Province
  B. Mapimi Superprovince
    1. Kaibabian Province
  C. Columbia Superprovince
    1. Columbian Province
    2. Artemisian Province

The fact that the six provinces in Utah were arranged in four different superprovinces underscores the patent faunal heterogeneity in Utah detailed below.

Durrant (1952) outlined "faunal subdivisions" of Utah as follows (also see Fig. 1):

I. Middle Rocky Mountain Faunal Area
  A. Wasatch Mountain Province
  B. Uinta Mountain Province
  C. High Plateau Province
    1. Northern High Plateau Subcenter
    2. Southern High Plateau Subcenter
II. Southern Rocky Mountain Faunal Area
  A. Coloradan Province
    1. La Sal Mountain Subcenter
    2. Abajo Mountain Subcenter
III. Colorado Plateau Faunal Area
  A. Canyonlands Province
    1. Kaiparowits Subcenter
    2. San Rafael Subcenter
    3. Grand Valley Subcenter
    4. San Juan Subcenter
    5. Painted Desert Subcenter
      a. Monument Valley District
      b. Navajo Mountain District
  B. Virgin River Valley Province
    1. Beaverdam Wash Subcenter
    2. St. George Subcenter

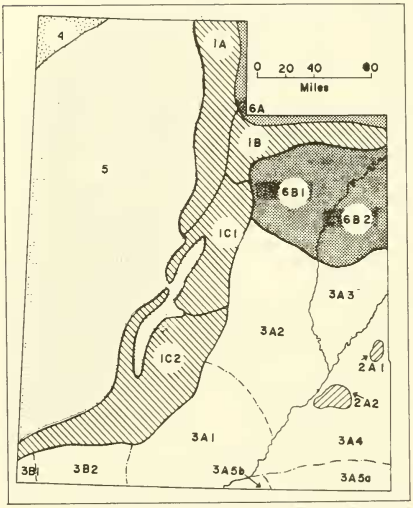

Fig. 1. Mammalian faunal subdivisions of Utah (after Durrant, 1952). For key to names of units, see text, p. 461.

IV. Columbia Plateau Faunal Area
V. Great Basin Faunal Area
VI. Northern Great Plains Faunal Area
 A. Bridger Basin Province
 B. Uinta Basin Province
  1. Duchesne Subcenter
  2. Uintah Subcenter

Durrant (1952) recognized these areas as distinctive because (1) certain species were restricted there and (2) because they acted as centers of differentiation for subspecies (p. 480). Boundaries of faunal areas were based on physiography. Although based mostly on distribution of mammals, Durrant's faunal areas are analogues of L. R. Dice's "biotic province," an ecogeographic unit that "... covers a considerable and continuous geographic area and is characterized by the occurrence of one or more ecologic associations that differ, at least in proportional area covered, from the associations in adjacent provinces" (Dice 1943: 3). Dice's units are based on distributional patterns in the biota as a whole, Durrant's on patterns in distribution and differentiation of mammals. Boundaries between both faunal areas and biotic provinces are zones of relatively rapid biotic change, zones in which limits of species tend to be concentrated (Armstrong 1972a). This fact was used in order to evaluate boundaries between faunal areas proposed by Durrant (1952: 480). A number of quantitative methods have been used in recent years to determine boundaries of faunal units, but faunal change in Utah is so rapid that useful units can be identified by inspection. Limits of ranges of 92 mammalian species were superimposed (Fig. 2). The concurrence between zones of rapid faunal change and ecogeographic boundaries is apparent from comparison of Figures 1 and 2. Each of the boundaries indicated in Durrant's map is marked by a concentration of limits in Figure 2. In particular, note the dense cluster of limits which outlines the central highlands and separates the Colorado Plateau on the east from the Great Basin in the west. In the northwestern corner of the state the Raft River Mountains are outlined clearly, as are the La Sal and Abajo Mountains in the southeast. A concentration of limits in the northeast suggests the distinctiveness of mammals of the Bridger Basin. In the west-central part of the state, the Deep Creek Mountains are highlighted by a concentration of limits. Were sufficient data available on mammals of this and other isolated mountain ranges of the Great Basin—comparable to those provided by Lee (1960) for the highlands of southeastern Utah—subdivisions of the Great Basin Faunal Area might be recognizable. It should be reemphasized that this evaluation of the boundaries of Durrant's faunal units is based on species' limits, whereas Durrant used two criteria, species' occurrence and differentiation of subspecies; this difference in technique has little bearing on the faunal units recognized.

Relationships among various faunal divisions of Utah were analyzed by a method used previously for Coloradan mammals (Armstrong 1972a). Occurrence of 109 mammalian species (92 species for which limits in Utah can be drawn with reasonable confidence and 17 species that range virtually statewide) was tabulated in each of

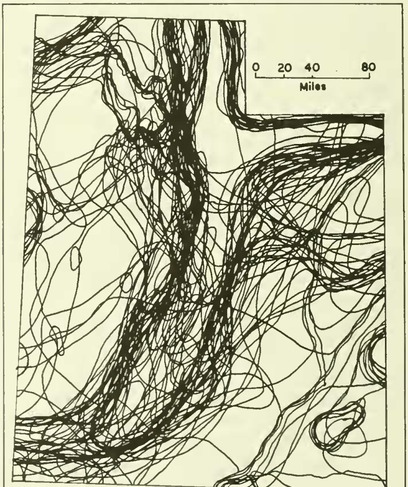

Fig. 2. Superimposed distributional limits in Utah of 92 mammalian species.

the 19 faunal units recognized by Durrant. Faunal resemblance was calculated by the formula $2C / N_1 + N_2$, where C is the number of species held in common between two units and N_1 and N_2 are total numbers of species in the two units. Resemblance values (which ranged from 0.438 to 0.964) were clustered by the unweighted pair-group method (Sokal and Sneath 1963: 309). Figure 3 is the result.

In large measure, the dendrogram substantiates the hierarchy of units suggested by Durrant (1952: 481—see p. 00 above), despite wide differences in technique and recent additions to knowledge of Utah mammals. Units of the Colorado Plateau form a tight cluster, with faunas of the Canyonlands and the Virgin River Valley separating into distinct subclusters, and units within the Canyonlands forming further subclusters east and west of the Colorado River. In the central mountainous core, two subclusters are evident. The Wasatch and Uinta mountains are more closely related than all but one other pair of faunal units, and the Northern High Plateaus and Southern High Plateaus form a distinct, albeit weaker, subcluster. The isolated La Sal and Abajo mountains form a distinct unit, allied (on average) more closely with the Colorado Plateau than with the central highlands of Utah. Their nearest contact with a well-developed highland fauna is via the high plateaus of western Colorado, not the Middle Rocky Mountains in Utah. The Duchesne and Uintah units of the Uinta Basin form a tight cluster and are distinct from faunal units of the Colorado Plateau south of the Tavaputs Plateaus, but they are more closely related to the Bridger Basin. The Great Basin and the Columbia Plateau (Raft River Mountains) tend to be faunally distinct from each other and from the rest of the state.

Comparison of Durrant's faunal units with the diagram in Figure 3 suggests that levels of the hierarchy (faunal area, province, subcenter, district) are not used quite consistently, at least at the specific level of analysis employed here. In particular, faunas of the Wasatch and Uinta Mountains are more closely related than most other pairs of units, yet they are distinguished as provinces. Recent studies (e.g., Durrant and Dean 1959) suggest that the Navajo Mountain and Monument Valley units are more distinctive than Durrant (1952) supposed. Indeed, Monument Valley seems to be more closely related to the San Juan area (which lies north of the San Juan River) than to the Navajo Mountain unit. Based on relationships in the dendrogram (Fig. 3), I suggest the following rough guidelines for levels of the hierarchy of ecogeographic units: average resemblance between faunal areas, less than 0.800; average resemblance between provinces within faunal areas, 0.800 to about 0.900; average resemblance between subcenters within provinces, greater than about 0.900. Using these criteria, the following slightly revised list of faunal subdivisions in Utah is suggested:

I. Central Highlands Faunal Area
   A. Middle Rocky Mountains Province
      1. Wasatch Mountains Subcenter
      2. Uinta Mountains Subcenter
   B. High Plateaus Province
      1. Northern High Plateaus Subcenter
      2. Southern High Plateaus Subcenter

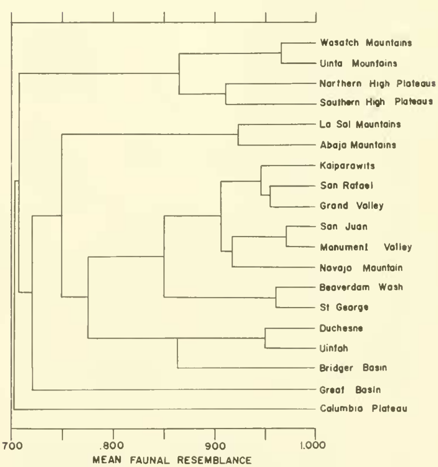

Fig. 3. Mean resemblance among mammalian faunal subdivisions of Utah. (For explanation of index, see text.)

II. Southern Rocky Mountains Faunal Area
   A. La Sal Mountains Subcenter
   B. Abajo Mountains Subcenter
III. Colorado Plateau Faunal Area
   A. Canyonlands Province
      1. Kaiparowits Subcenter
      2. San Rafael Subcenter
      3. Grand Valley Subcenter
      4. San Juan Subcenter
      5. Monument Valley Subcenter
      6. Navajo Mountain Subcenter
      Virgin River Valley Province
      1. Beaverdam Wash Subcenter
      2. St. George Subcenter
IV. Columbia Plateau Faunal Area
V. Great Basin Faunal Area
VI. Wyoming Basin Faunal Area
   A. Bridger Basin Province
   B. Uinta Basin Province
      1. Uinta Subcenter
      2. Duchesne Subcenter

Changes in names of two faunal areas (Middle Rocky Mountains to Central Highlands, Northern Great Plains to Wyoming Basin) follow Durrant's lead in naming faunal units to correspond with physiographic units (here following Fenneman, 1931).

Areographic Patterns.— Having considered distributional patterns of mammals in Utah and arrived at a set of ecogeographic faunal areas, let us turn to broader, continental patterns of distribution. The pattern of species' ranges, irrespective of extant ecologic pattern, may suggest historic affinities of the fauna. Udvardy (1969: 282) noted that the constituent species of a faunal list "... fall into groups with respect to the shapes of their geographic areas." These groups of species may be called "faunal elements." Polunin (1960: 212) suggested sorting out elements in a local flora as follows: (1) remove exotic and occasional species; (2) remove widespread species; (3) remove endemic species; and (4) sort out the remainder according to the shapes of their ranges. Such a procedure was used here, resulting in nine distinctive, areographic faunal elements and a group of widespread species.

The implications of these areographic faunal elements are complex. The area occupied summarizes the interaction of species' limits of tolerance with the mosaic of regional landscapes; both are subject to change over time. Hultén (1937) argued strongly that areographic analysis leads to historical insights in plant geography, promulgating the concept of "progressive equiformal areas," the common centers of which point to areas of origin (or refugia from environmental purturbations). Broad areographic studies of animals (e.g., Dunn 1931, for North American amphibians and reptiles, Mayr 1946, for birds, and Simpson 1947, and Burt 1958, for mammals) have used ranges—usually of higher taxonomic categories—as a basis for historical conclusions. A few studies have sought to use areographic patterns of species as clues to local faunal history. For example, Miller (1951: 582) recognized four avifaunal elements in California, "... on the basis of strong or repeated associations of species which have similar centers of distribution and probably also similar areas of origin." Armstrong (1972a: 333) discussed areographic patterns of Coloradan mammals, drawing tentative historical conclusions. Clearly, faunal elements may have a degree of historic integrity, reflecting centers of origin and dispersal, although recent ecologic history may have distorted older patterns. Despite problems in interpretation, the attempt to sort out areographic faunal elements is important. In the absence of a fossil record, such an exercise may provide the only clues to the development of the extant fauna.

Seventeen species (14 percent of the Utahan mammalian fauna) have ranges centering on the Middle Rocky Mountains (see Fig. 4A) and are called Cordilleran species. These are:

Sorex vagrans—Vagrant Shrew
Sorex monticolus—Dusky Shrew
Sorex nanus—Dwarf Shrew
Ochotona princeps—Pika
Eutamias amoenus—Yellow-pine Chipmunk
Eutamias umbrinus—Uinta Chipmunk
Marmota flaviventris—Yellow-bellied Marmot
Spermophilus armatus—Uinta Ground Squirrel
Spermophilus lateralis—Golden-mantled Ground Squirrel
Thomomys talpoides—Northern Pocket Gopher
Neotoma cinerea—Bushy-tailed Woodrat

Microtus montanus—Montane Vole
Microtus longicaudus—Long-tailed Vole
Arvicola richardsoni—Water Vole
Zapus princeps—Western Jumping Mouse
Ovis canadensis—Bighorn Sheep
Bison bison—Bison

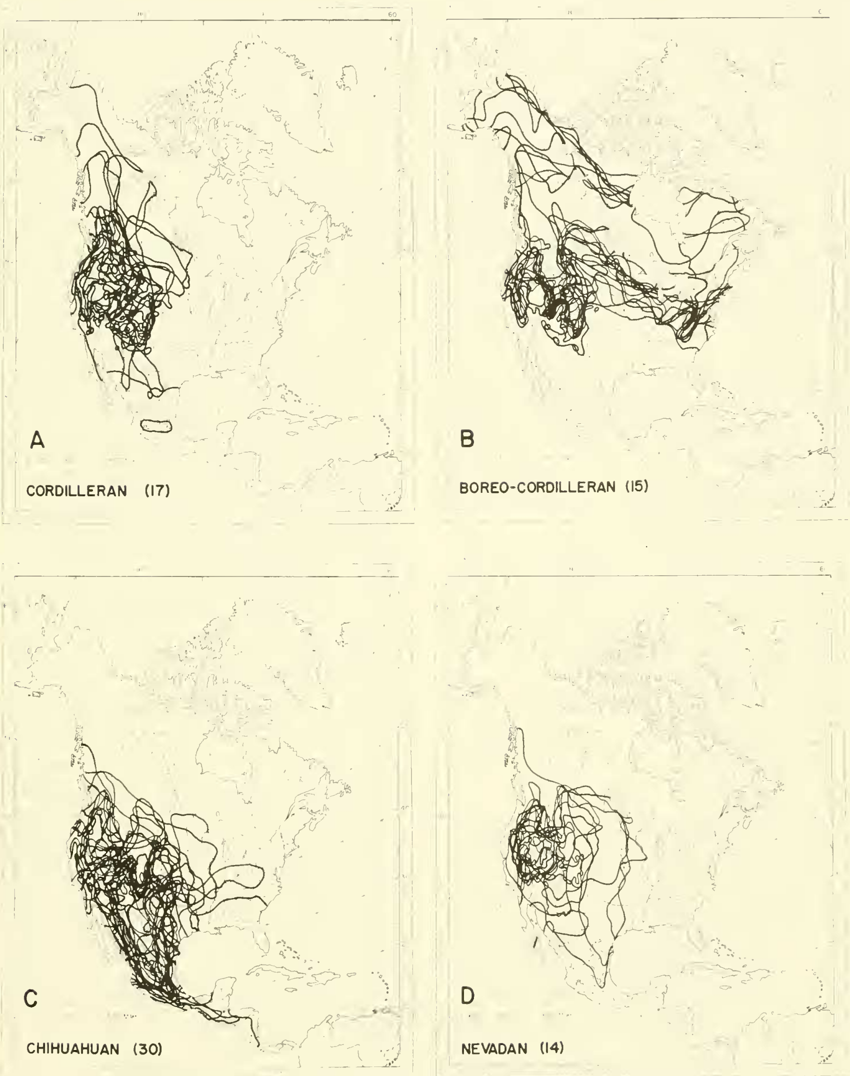

Fig. 4 A-D. Superimposed continental distributions of species of four areographic faunal elements.

Ranges of most of these species extend from the Canadian Rockies southward, often in an increasingly insular pattern, to Arizona and New Mexico. They are restricted at their southern limits to mountainous country. Habitat of many of the species is mountain meadows, streamsides, and forest-edge situations. Two of the species (*Sorex obscurus* and *Spermophilus lateralis*) have isolated montane populations in Mexico. However, four other species (*Sorex vagrans*, *Eutamias amoenus*, *Spermophilus armatus*, and *Arvicola richardsoni*) do not extend farther south than the Middle Rocky Mountains, and they do not reach Colorado. The American bison of Utah were members of the subspecies *Bison bison athabascae* (see Hall and Kelson 1959: 1025) and hence are included as Cordilleran rather than widespread species.

The following 15 species of Utahan mammals (12 percent of the fauna) share a distributional pattern that may be called Boreo-Cordilleran:

Sorex cinereus—Masked Shrew
Sorex palustris—Water Shrew
Lepus americanus—Snowshoe Hare
Eutamias minimus—Least Chipmunk
Tamiasciurus hudsonicus—Red Squirrel, or Chickaree
Glaucomys sabrinus—Northern Flying Squirrel
Clethrionomys gapperi—Southern Red-backed Vole
Phenacomys intermedius—Heather Vole
Microtus pennsylvanicus—Meadow Vole
Martes americana—Marten
Martes pennanti—Fisher
Mustela erminea—Ermine
Gulo gulo—Wolverine
Felis lynx—Lynx
Alces alces—Moose

These species are distributed in mountainous parts of western North America and also eastward across the continent, mostly in forested areas (Fig. 4B). In an areographic sense, these species contrast markedly with those of the Cordilleran Faunal Element. Unlike Cordilleran species, many Boreo-Cordilleran mammals range throughout forested parts of Alaska and several species (including *Sorex cinereus*, *Mustela erminea*, *Gulo gulo*, *Felis lynx*, *Alces alces*) occur on both sides of Bering Strait. In addition, there is a tendency for Boreo-Cordilleran mammals to be associated with heavy forest. There is some suggestion that *Eutamias minimus*, perhaps the most euryecious mammal in this faunal element, may include more than a single species (Sutton and Nadler, 1969).

Thirty species (24 percent of the fauna) comprise the Chihuahuan Faunal Element:

Notiosorex crawfordi—Desert Shrew
Myotis californicus—California Myotis
Myotis yumanensis—Yuma Myotis
Myotis velifer—Cave Myotis
Myotis evotis—Long-eared Myotis
Myotis thysanodes—Fringed Myotis
Pipistrellus hesperus—Western Pipistrelle
Plecotus townsendii—Townsend's Big-eared Bat
Idionycteris phyllotis—Allen's Big-eared Bat
Antrozous pallidus—Pallid Bat
Tadarida brasiliensis—Brazilian Free-tailed Bat
Tadarida macrotis—Big Free-tailed Bat
Sylvilagus audubonii—Desert Cottontail
Lepus californicus—Black-tailed Jackrabbit
Eutamias dorsalis—Cliff Chipmunk
Spermophilus spilosoma—Spotted Ground Squirrel
Spermophilus variegatus—Rock Squirrel
Perognathus flavus—Silky Pocket Mouse
Dipodomys ordii—Ord's Kangaroo Rat
Reithrodontomys megalotis—Western Harvest Mouse
Peromyscus boylii—Brush Mouse
Peromyscus truei—Pinyon Mouse
Peromyscus difficilis—Rock Mouse
Neotoma albigula—White-throated Woodrat
Neotoma mexicana—Mexican Woodrat
Microtus mexicanus—Mexican Vole
Vulpes macrotis—Kit Fox
Urocyon cinereoargenteus—Gray Fox
Bassariscus astutus—Ringtail
Spilogale gracilis—Western Spotted Skunk

These species mostly occur in arid to semiarid grasslands or in rocky, broken brushlands or woodlands. They share a center of coincidence in the basin and range region of Chihuahua and Coahuila, Mexico, and Trans-Pecos Texas (Fig. 4C). Of this faunal element, four species (*Plecotus townsendii*, *Tadarida brasiliensis*, *Reithrodontomys megalotis*, and *Urocyon cinereoargenteus*) range east of the Mississippi River. However, their identification in the southwest with this faunal element is clear. The two species of free-tailed bats, *Tadarida brasiliensis* and *T. macrotis*, occur widely in South America, as does *Urocyon cine-*

reoargenteus. These might have been segregated as a Neotropical Faunal Element, inasmuch as only four of the remaining Chihuahuan species *(Myotis velifer, Peromyscus boylii, Neotoma mexicana, Spilogale gracilis)* range farther south than the Isthmus of Tehuantepec. Note that 12 of the Chihuahuan species (40 percent) are bats. Despite their capacity for flight these species are of restricted distribution, present patterns perhaps reflecting the historical integrity of this faunal element.

A Nevadan Faunal Element (Fig. 4D), comprised of the following 14 species, with a center of coincidence in Nevada, contributes 11 percent of the Utahan fauna:

Sorex merriami—Merriam's Shrew
Myotis volans—Long-legged Myotis
Euderma maculatum—Spotted Bat
Sylvilagus idahoensis—Pygmy Rabbit
Sylvilagus nuttallii—Nuttall's Cottontail
Lepus townsendii—White-tailed Jackrabbit
Spermophilus townsendii—Townsend's Ground Squirrel
Spermophilus beldingi—Belding's Ground Squirrel
Perognathus parvus—Great Basin Pocket Mouse
Microdipodops megacephalus—Dark Kangaroo Mouse
Dipodomys microps—Chisel-toothed Kangaroo Rat
Onychomys leucogaster—Northern Grasshopper Mouse
Lagurus curtatus—Sagebrush Vole
Antilocapra americana—Pronghorn

This is a complex distributional element. At a finer level of analysis it might be subdivided profitably. Some species are restricted to arid interior basins of the western United States (e.g., *Spermophilus townsendii, Microdipodops megacephalus, Dipodomys microps*), whereas others inhabit sagebrush steppe (e.g., *Sorex merriami, Sylvilagus idahoensis, Sylvilagus nuttallii, Lagurus curtatus*). *Lepus townsendii, Onychomys leucogaster,* and *Antilocapra americana* have an additional center of cooccurrence on the central Great Plains and might be considered a part of a Campestrian Faunal Element (Armstrong 1972a: 356), although this designation would not be particularly meaningful with respect to these species as they occur in Utah, inasmuch as communication with the Great Plains is indirect.

Twelve species (10 percent of the fauna) have continental distributions that might be called "Yuman," for their center of coincidence is in the Mojave Desert and along the Lower Colorado River in California, Arizona, Sonora, and Baja California (Fig. 4F). These species are:

Ammospermophilus leucurus—White-tailed Antelope Squirrel
Thomomys bottae—Botta's Pocket Gopher
Perognathus longimembris—Little Pocket Mouse
Perognathus formosus—Long-tailed Pocket Mouse
Perognathus penicillatus—Desert Pocket Mouse
Perognathus intermedius—Rock Pocket Mouse
Dipodomys deserti—Desert Kangaroo Rat
Dipodomys merriami—Merriam's Kangaroo Rat
Peromyscus eremicus—Cactus Mouse
Peromyscus crinitus—Canyon Mouse
Onychomys torridus—Southern Grasshopper Mouse
Neotoma lepida—Desert Woodrat

In the vicinity of the center of coincidence, *Ammospermophilus leucurus* and *Perognathus formosus* only occur west of the Colorado River, and *Perognathus intermedius* is known only east of the river. Yuman mammals generally do not range southward in Mexico as far as Chihuahuan species, with only five reaching Jalisco, Guanajuato, and San Luis Potosí. On the north, most species reach no farther than southeastern Oregon and southwestern Idaho, and several reach limits in Nevada and Utah. Note that half the species in this faunal element are heteromyid rodents, whereas the predominant rodents in the Chihuahuan element are cricetids. This fact underscores the historical integrity of these faunal elements.

Five species, comprising 4 percent of the Utahan mammalian fauna, constitute an Arizonan Faunal Element (Fig. 4F). These are:

Eutamias quadrivittatus—Colorado Chipmunk
Cynomys gunnisoni—Gunnison's Prairie Dog
Sciurus aberti—Abert's Squirrel
Perognathus apache—Apache Pocket Mouse
Neotoma stephensi—Stephens' Woodrat

These are species of the Four Corners area (although *Neotoma stephensi* is as yet unknown from Colorado, Armstrong 1972a: 312). In Utah, Arizonan species generally are restricted to the southeastern part of the state; all but *E. quadrivittatus* occur only east of the Colorado and Green rivers.

Three mammals of the Great Plains (*Spermophilus tridecemlineatus, Perognathus fasciatus, Mustela nigripes*) have limited

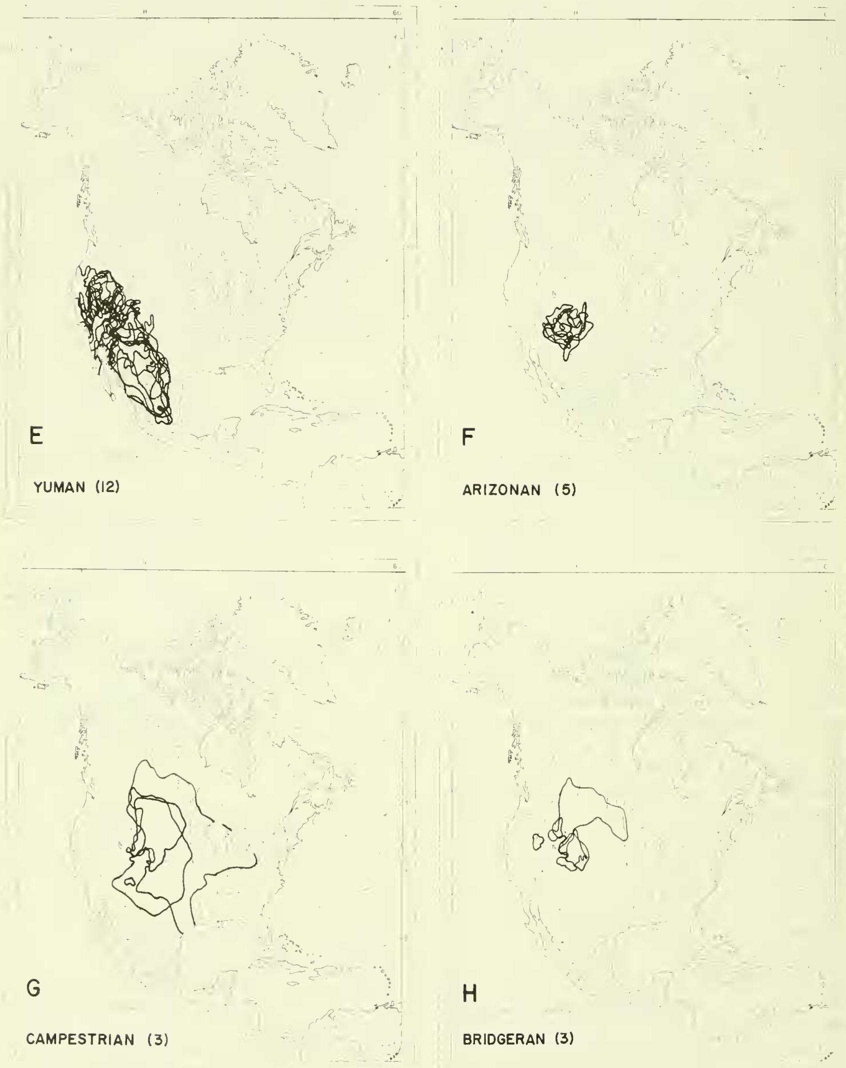

Fig. 4 E-H. Superimposed continental distributions of species of four areograhic faunal elements.

ranges in Utah and constitute a Campestrian Faunal Element (Fig. 4G). All occur in grasslands of the eastern part of the state. Another three species (*Cynomys leucurus*, *Thomomys idahoensis*, and *Spermophilus richardsonii*) share a center of coincidence in the Bridger Basin of southwestern Wyoming (Fig. 4H) and are herein called the Bridgeran Faunal Element. Armstrong (1972a: 354) placed *S. richardsonii* as a member of the Cordilleran Faunal Element, but its range is somewhat discordant with that group of species. Recent studies (Nadler et al. 1971) suggest that the population in Wyoming, Utah, and Colorado, known as *S. r. elegans*, is in fact specifically distinct from *S. richardsonii*. The range of *elegans* fits closely with the Bridgeran Faunal Element.

A single species of the mammalian fauna of Utah is obviously endemic there, *Cynomys parvidens*, the Utah Prairie Dog. According to Pizzimenti and Collier (1973), *C. parvidens* is more closely related to *C. leucurus* (a species of the Bridgeran Faunal Element) than to other prairie dogs; Collier and Spillett (1975) concluded that the range of the *C. parvidens* once covered large portions of the Great Basin.

Of mammals of Utah, the following 26 kinds (21 percent of the state's fauna) are sufficiently widespread (Fig. 4I) that they cannot be identified with any one areographic faunal element:

Myotis lucifugus—Little Brown Bat
Myotis leibii—Small-footed Bat
Lasionycteris noctivagans—Silver-haired Bat
Eptesicus fuscus—Big Brown Bat
Lasiurus cinereus—Hoary Bat
Lasiurus borealis—Red Bat
Castor canadensis—Beaver
Peromyscus maniculatus—Deer Mouse
Ondatra zibethicus—Muskrat
Erethizon dorsatum—Porcupine
Canis latrans—Coyote
Canis lupus—Gray Wolf
Vulpes vulpes—Red Fox
Ursus americanus—Black Bear
Ursus arctos—Grizzly Bear
Procyon lotor—Raccoon
Mustela frenata—Long-tailed Weasel
Mustela vison—Mink
Mephitis mephitis—Striped Skunk
Taxidea taxus—Badger
Lutra canadensis—River Otter
Felis concolor—Mountain Lion
Felis rufus—Bobcat
Cervus elaphus—Wapiti, or American Elk
Odocoileus hemionus—Mule Deer
Odocoileus virginianus—White-tailed Deer

Many of these species are rather large in size and many have broad habitat tolerances. It is perhaps noteworthy that half of these eurychores are members of a single order, Carnivora; carnivores are at least one step removed from direct dependence on the vegetation for food and generally are less narrowly restricted to particular habitats than are herbivores. Thirteen of the 23 carnivores known to occur in Utah are widespread species. In addition, three of four Utahn cervids are widespread on a continental scale. Three highly specialized aquatic species, the beaver, the muskrat, and the mink, appear on the list. This is hardly surprising, since aquatic habitats provide corridors of uniform habitat for dispersal through otherwise highly distinctive regions. Fewer than one-third of Utah's bats are widespread species; nearly 60 percent

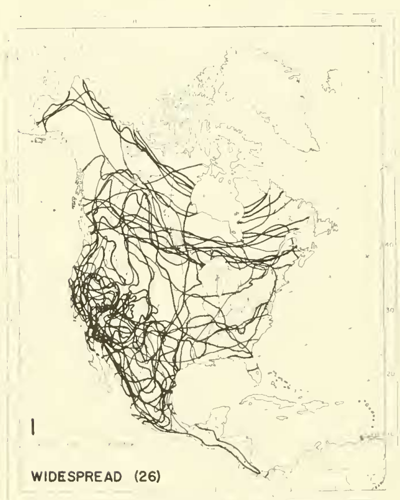

Fig. 4 I. Superimposed continental distributions of 26 widespread species.

are Chihauhuan kinds. Were distribution of bats better known, they might provide quite useful data for zoogeographers, contrary to the conventional wisdom.

The least broadly distributed species on the above list are the small-footed myotis (*Myotis leibii*) and the grizzly bear (*Ursus arctos*). The range of the former species is similar to that of those labelled "Nevadan," but it extends also across the Great Plains to the Ohio Valley and the East Coast. The former range of the grizzly bear extended eastward across the Northern Great Plains and Central Great Plains; otherwise the range is that of a Cordilleran species.

Figure 5 indicates cumulative percentage composition of the mammalian faunas of 19 ecogeographic faunal units by species of the 10 faunal elements identified by areographic analysis. Also indicated, for comparison, is the composition of the fauna of Utah as a whole, based on a total of 126 species. Only 109 species were tabulated in the faunal units, because of inadequate distributional data on 17 species (see Methods, above). Those species too poorly known to map represent five faunal elements: Cordilleran (three species), Boreo-cordilleran (one), Chihuahuan (four), Nevadan (three), and widespread (six). Thus, poorly known species are sufficiently well distributed across the major faunal elements that they do not bias the remarks that follow.

Note first in Figure 5 the consistent importance of widespread species at about 35 percent (28 to 38) through each of the faunal elements. It is the differential occurrence of species of well-defined areographic elements that makes the faunal units distinctive. Cordilleran species are most important in faunal units of the central mountain core of the state, somewhat less important in the La Sal Mountains and the Raft River Mountains of the Columbia Plateau. In other faunal units, their contribution falls to 10 percent or less. Boreo-cordilleran species are even more narrowly restricted to mountainous areas, although one species, *Eutamias minimus*, is sufficiently euryecious that it occurs in most faunal areas. "Boreal" mammals of Utah discussed by Brown (in press) mostly are Cordilleran and Boreo-cordilleran species as defined here.

The Chihuahuan Faunal Element is the largest distinctive areographic element in Utah, constituting about one quarter of the fauna. Given this prominence statewide, the element is under-represented in the central highlands faunal areas and on the Columbia Plateau. Over most of the Colorado Plateau south of the Tavaputs Plateaus, the Chihuahuan element contributes some 40 percent of the fauna. North of the Tavaputs Plateaus, in the southeastern mountains, and in the Great Basin, the importance of Chihuahuan species is diminished. Yuman mammals are most important on the southern Colorado Plateau, especially in the Virgin River Valley. They are absent from the Middle Rocky Mountain Province and from the Northern High Plateaus. Nevadan species, on the other hand, are most important in the Great Basin, with modest representation over most of the rest of the state (except on the Colorado Plateau, where they tend to be under-represented). The minor faunal elements tend to show rather narrow distribution across the state. Campestrian species occur in eastern Utah. Arizonan species occur mostly in the Canyonlands Province of the Colorado Plateau and in the Uinta Basin. Bridgeran species occur only in northeastern and east-central parts of the state.

Having considered the composition of the faunas of the ecogeographic units, it might be useful (if only as a check on the integrity of the faunal elements) to look briefly at the extent to which members of the 10 faunal elements occupy the various units (Table 1). Most of the units include 60 to 70 percent of the widespread species, with highest percentages occurring in mountainous areas. As might be expected, the units of the Central Highlands Faunal Area accommodate most members of the Cordilleran and Boreo-cordilleran elements, with occurrence attenuating southward. The Colorado Plateau includes the ranges of the highest proportion of Chihuahuan species. Yuman species, by contrast, occur strongly only in the Virgin River Valley, and Nevadan mammals are well represented only in the Great Basin. The minor faunal elements also are strongly represented only in local areas—Campestrian species in the northeast, Arizonan species east of the Colorado River (and south of its confluence with the Green River), the Bridgeran species in the Bridger Basin.

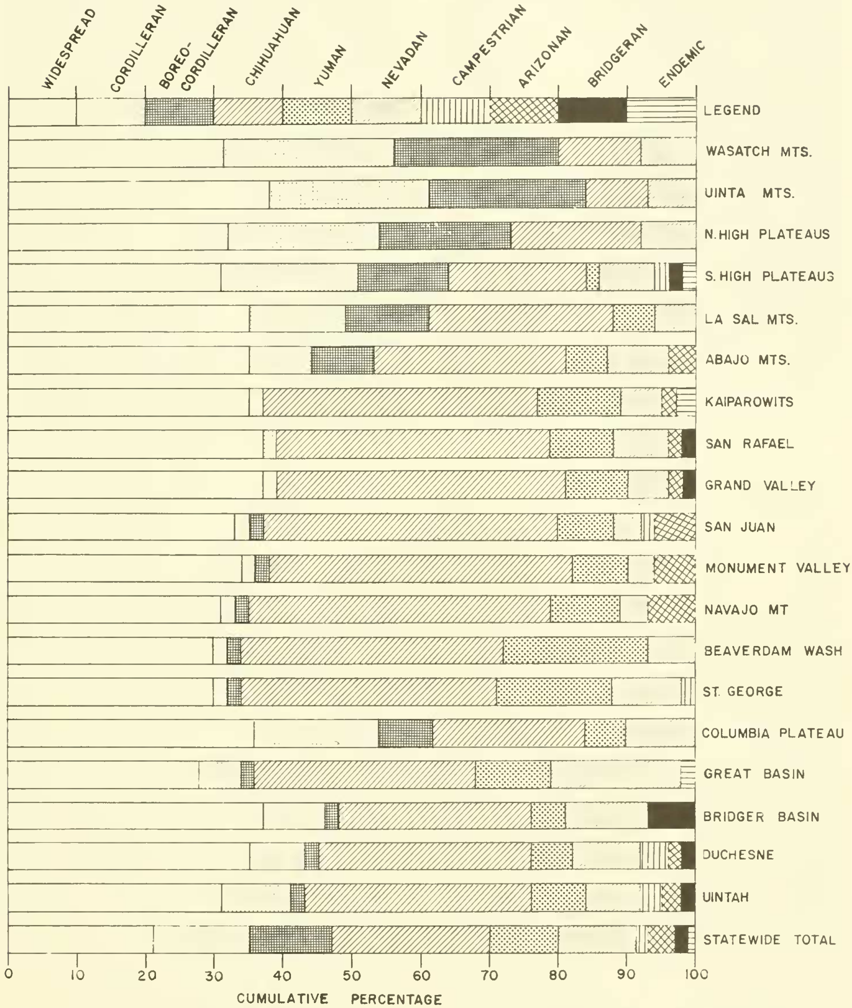

Fig. 5. Cumulative percentage composition of mammalian faunas of ecogeographic faunal areas by members of ten areographic faunal elements.

Historical Implications.— One of the major goals of zoogeographic analysis is to gain some insight into the evolution of local or regional faunas. Indeed, in the absence of an adequate fossil record, extant patterns of distribution and differentiation provide the only historical data that we have to work with. Durrant (1952) looked at patterns of subspecific differentiation in fossorial rodents as a clue to the Pleistocene history of the Bonneville Basin. Lee (1960) studied the distribution and differentiation of montane mammals of southeastern Utah and drew inferences about past faunal movements. Findley (1969) presented a strong argument on historical implications of such patterns in New Mexico and adjacent areas. Brown (1971, in press) analyzed distribution on several mountain ranges in Utah of mammals typical of woodland (and higher elevation) biotic communities, arguing convincingly that extant distributional patterns stem from local extinction of populations that reached the montane islands during the late Pleistocene. Armstrong (1972a) relied on evidence at both the specific and subspecific level to reach tentative historical conclusions about Coloradan mammals, and hypothesized access to the state by several faunal components under a diversity of environmental conditions which prevailed at various times in the past.

Extant zoogeographic patterns in western North America are a post-Pleistocene development. The Pleistocene Epoch was marked by pronounced climatic fluctuations. Warm, dry periods were interrupted by cool, moist glacio-pluvial intervals. Evidences of zoogeographic patterns in the earlier Pleistocene were obliterated by the last major glacial interval, the subsequent Hypsithermal Interval (Deevey and Flint 1957), and the development of the existing climatic regime (Armstrong 1972a). Extant patterns may provide clues to these most recent events. In the absence of a coherent or extensive fossil record, distributional patterns of recent species are the only clues available to

Table 1. Percentage of members of areographic faunal elements occurring in ecogeographic faunal units.

	Widespread	Cordilleran	Boreo-cordilleran	Chihuahuan	Yuman	Nevadan	Campestrian	Arizonan	Bridgeran	Endemic
Wasatch Mountains	69	82	93	23	—	29	—	—	—	—
Uinta Mountains	77	71	80	17	—	29	—	—	—	—
Northern High Plateaus	73	71	79	37	—	36	—	—	—	—
Southern High Plateaus	65	65	47	37	8	36	33	—	33	100
La Sal Mountains	69	47	40	43	25	21	—	—	—	—
Abajo Mountains	62	24	27	43	25	29	—	40	—	—
Kaiparowits	65	6	—	63	50	21	—	20	33	—
San Rafael	65	6	—	60	33	21	—	20	33	—
Grand Valley	65	6	—	63	33	14	—	20	33	—
San Juan	65	6	7	73	33	14	33	60	—	—
Monument Valley	65	6	7	73	33	14	—	60	—	—
Navajo	62	6	7	77	42	14	—	80	—	—
Beaverdam	62	6	7	67	92	29	—	—	—	—
St. George	58	6	7	60	75	29	33	—	—	—
Columbia Plateau	69	53	27	37	25	36	—	—	—	—
Great Basin	58	18	7	57	50	71	—	—	—	100
Bridger	62	24	7	25	17	36	—	—	100	—
Duchesne	65	24	7	50	25	36	67	20	33	—
Uintah	62	29	7	57	33	29	67	40	33	—

us. This is the case in Utah. Conspicuously lacking from the abundant literature on Pleistocene environments of Utah is any record of a mammalian local fauna. Even fragmentary fossils are few. When a nearly adequate fossil local fauna does become available (the Hogup Cave deposits from Box Elder County described by Durrant, 1970, and dated at 8500 years B.P.) the mammals that are present are those that would be expected in the vicinity of the cave today.

For purposes of discussion of Pleistocene conditions, Utah is conveniently divisible into three broad sections: the Great Basin, the central mountainous core, and the Colorado Plateau. The Great Basin records evidence of a series of pluvial periods separated by intervals of dessication (for details, see Morrison 1965). Lake levels fluctuated in synchrony with alpine glaciers in the higher mountains of central and northern Utah. This glaciation strongly influenced the modern landscape, lowering regional snowlines some 4000 ft, and producing summer temperatures perhaps 16 F cooler than today (Richmond 1965). On the Colorado Plateau, glacial intervals were marked by erosion, and warmer, drier periods produced sedimentary deposition (Kottlowski, Cooley, and Ruhe 1965). These events and conditions set an environmental baseline against which present distributional patterns of mammals have developed. During the last glacio-pluvial stage, conditions probably prevailed that were beyond the tolerance of many species in the fauna today. Previous patterns of distribution would have been obscured. With a depression of zonal biotic communities, forested situations that are highly disjunct today would have been more nearly continuous, and semidesert and desert community-types would have seen concommitant restriction and fragmentation.

The present-day fauna of the highlands of Utah provides better evidence of past environmental change than do faunas of the Colorado Plateau and the Great Basin. Today, a number of the state's mountain ranges and high plateaus appear as "islands" in a "sea" of nonmontane habitats. Communication among them by nonvolant mammals restricted to forested habitats is probably impossible. Nonetheless, some of the highlands have reasonably complete highland faunas (Brown 1971, in press). Altitudinal depression of zonal biotic communities by 2000 to 4000 ft would unite many of these areas with corridors of suitable habitat. The La Sal Mountains would have been connected with the Uncompahgre Plateau and the San Juan Mountains (and nearby ranges), and the Abajo Mountains probably would have been joined with the La Sals by more-or-less continuous forest or woodland corridors. Navajo Mountain, south of the San Juan River, and the Henry Mountains probably have been isolated (or nearly so) throughout Pleistocene times (although Lee, 1960, noted some affinity of mammals of the Henrys with those of the Aquarius Plateau). The distribution of forest-dwelling mammals along the mountains of central Utah suggests that Pleistocene conditions there provided a continuous corridor for movement. Isolated ranges of the Great Basin generally support depauperate highland faunas (Brown 1971, in press), although the definitive study of mammals of the minor ranges of southwestern Utah (House Range, Wah Wah Mountains, etc.) remains to be made.

The fact that faunas of the more isolated ranges on either side of the central highlands corridor have variously depauperate faunas probably reflects local extinction rather than selective or chance dispersal across barriers. The fact that such extinction has been more pronounced on the smaller uplifts may reflect the greater susceptibility of small populations to extinction (Brown 1971, in press). Such small populations would have been constricted still further by the climatic changes of the Hypsithermal Interval (warmer and effectively or absolutely drier than at present) which would have resulted in upward movement of zonal biotic communities with consequent restriction of the higher zones.

At lower elevations in Utah, extant distributional patterns strongly reflect present-day physiography, suggesting the efficacy of existing boundaries throughout the period of development of the fauna. Ranges of many Chihuahuan and Yuman species, for example, are limited on the Colorado Plateau by the major rivers and their canyons, despite the fact that seemingly suitable habitat often exists on the other side of the barrier. On a north-south axis, the Wasatch Mountains and the high plateaus today form an effective barrier to communication between the Great Basin and the Colorado Plateau. This barrier seems to have been generally effective throughout the period of evolution of the fauna. If the Hypsithermal Interval had significantly reduced its effectiveness, one would expect to find several Nevadan species on the Colorado Plateau. However, only the most euryecious species are found on both sides of the mountains. The Uinta Mountains also seem to have persisted as an effective barrier as faunal patterns have evolved. Bridgeran species are not found on the Colorado Plateau to any significant extent, and most Chihuahuan species are limited south of the Uintas.

A barrier to one faunal element or species may well be a corridor for the movement of another. The central mountainous corridor has been discussed in this context. The river systems of the Colorado Plateau seem generally to have been ineffective as corridors. Often they are entrenched deeply; riparian habitats tend to be fragmented or nonexistent. Species adapted to the broken habitats of the canyons seem to have found the river systems more effective corridors than have species of desert grasslands (such as several Yuman species).

Kelson (1951) suggested that the Colorado-Green system becomes an increasingly less effective zoogeographic barrier northward. East of the Colorado River and north of the San Juan, there is no strong barrier to northward faunal movement until one reaches the Book Cliffs. West of the Colorado, the Kaiparowits Plateau and the canyon of the Escalante River may constitute major barriers, but the mammals of this area remain poorly known except in the immediate vicinity of Lake Powell.

In summary, scrutiny of broad patterns of distribution of mammalian species provides few clues to the conditions of the past that influenced the composition of the extant fauna. Ranges of montane mammals suggest the occurrence of more continuous highland biotic communities in late Pleistocene time, and the depauperate faunas of isolated ranges may reflect the efficacy of the Hypsithermal Interval in constricting highland communities more severely than at present. In the lowlands, distributions correspond to extant barriers. Truly relict populations of lowland, xeric-adapted species are lacking. The overall conclusion must be that barriers to distribution in the present also were barriers to distribution in the past.

Summary

Distributional patterns of the 126 mammalian species native to Utah were analyzed and discussed. Ecogeographic faunal areas, proposed by Durrant (1952), were reevaluated. These correspond strongly with physiographic subdivisions of Utah. Areographic analysis indicated that several faunal elements contribute to the total mammalian assemblage within the political confines of Utah. These faunal elements contribute differentially to the several ecogeographic units, and they differ in their response to barriers and corridors for dispersal. With the exception of the montane fauna of the highlands of the state—which reflects both a cooler, moister late Pleistocene climate, and a warmer, effectively drier Hypsithermal climate—clues are lacking to suggest the vagaries of Quaternary history. Data still are inadequate to allow a satisfactory picture of some aspects of mammalian zoogeography in Utah. Areas of particular interest are the south-central part of the state (Kaiparowits Subcenter) and the isolated basins and ranges of the southern part of the Great Basin Faunal Area.

Literature Cited

Allen, J. A. 1892. The geographical distribution of North American mammals. Bull. Amer. Mus. Nat. Hist. 4: 199–243.

Anderson, S. 1955. An additional record of *Mustela erminea* from Utah. J. Mamm. 36: 568.

______. 1959. Distribution, variation, and relationships of the montane vole, Microtus montanus. Univ. Kansas Publ., Mus. Nat. Hist. 9: 415-511.

Armstrong, D. M. 1972a. Distribution of mammals in Colorado. Monogr., Univ. Kansas Mus. Nat. Hist. 3: x + 1-415.

______. 1972b. Mammals of Canyonlands National Park, Utah, I. Preliminary report of investigations, June-July 1972. Processed report for National Park Service, U.S. Dept. of Interior, 22pp.

______. 1973. Preliminary observations on mammalian faunal relationships, Canyonlands National Park, Utah. J. Colorado-Wyoming Acad. Sci. 7(4): 41-42.

______. 1974. Second record of the Mexican big-eared bat in Utah. Southw. Nat. 19: 114.

Behle, W. H., and R. M. Hansen. 1951. Notes on the short-tailed weasel in Utah. J. Mamm. 32: 226-227.

Benson, S. B. 1954. Records of the spotted bat (*Euderma maculata*) from California and Utah. J. Mamm. 35: 117.

Black, H. L. 1970. Occurrence of the Mexican big-eared bat in Utah. J. Mamm. 51: 190.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. Amer. Nat. 105: 467-478.

______. In press. The theory of insular biogeography and the distribution of boreal birds and mammals. Great Basin Nat. Mem. 2: 209-227.

Burt, W. H. 1958. The history and affinities of the recent land mammals of western North America. Publ., Amer. Assoc. Adv. Sci. 51: 131-154.

Cockrum, E. L. 1960. The recent mammals of Arizona: their taxonomy and distribution. Univ. Arizona Press, Tucson, viii + 276 pp.

Collier, G. D., and J. J. Spillett. 1975. Factors influencing the distribution of the Utah prairie dog, *Cynomys parvidens* (Sciuridae). Southw. Nat., 20: 151-158.

Davis, W. B. 1939. The recent mammals of Idaho. Caxton Printers, Caldwell, 400 pp.

Dearden, L. C., and M. R. Lee. 1955. A new sagebrush vole, genus *Lagurus*, from Utah. J. Mamm. 36: 270-273.

Deevey, E. S., Jr., and R. F. Flint. 1957. Postglacial Hypsithermal Interval. Science 125: 182-184.

Dice, L. R. 1943. The Biotic Provinces of North America. Univ. of Michigan Press, Ann Arbor, viii + 78 pp.

Dunn, E. R. 1931. The herpetological fauna of the Americas. Copeia 1931: 106-119.

Durrant, S. D. 1952. Mammals of Utah, taxonomy and distribution. Univ. Kansas Publ., Mus. Nat. Hist. 6: 1-549.

______. 1970. Faunal remains as indicators of Neothermal climates at Hogup Cave. Anthro. Papers, Univ. Utah 93: 241-245.

Durrant, S. D., and N. K. Dean. 1959. Mammals of Glen Canyon. Anthro. Papers, Univ. Utah 40: 73-106.

______. 1960. Mammals of Flaming Gorge Reservoir Basin. Anthro. Papers, Univ. Utah 48: 209-235.

Durrant, S. D., and R. M. Hansen. 1954. Taxonomy of the chickarees (*Tamiasciurus*) of Utah. J. Mamm. 35: 87-95.

Durrant, S. D., and M. R. Lee. 1955. Rare shrews from Utah and Wyoming. J. Mamm. 36: 560-561.

______. 1956. A new pocket mouse from southeastern Utah. Proc. Biol. Soc. Washington 69: 183-186.

Durrant, S. D., M. R. Lee, and R. M. Hansen. 1955. Additional records and extensions of ranges of mammals from Utah. Univ. Kansas Publ., Mus. Nat. Hist. 9: 69-80.

Durrant, S. D., and J. P. Newey. 1953. Masked shrew, *Sorex cinereus*, in Utah. J. Mamm. 54: 116-117.

Easterla, D. A. 1965. The spotted bat in Utah. J. Mamm. 46: 665-668.

______. 1966. Yuma myotis and fringed myotis in southern Utah. J. Mamm. 47: 350-351.

Egoscue, H. J. 1961. Small mammal records from western Utah. J. Mamm. 43: 122-123.

______. 1965. Records of shrews, voles, chipmunks, cottontails, and mountain sheep from Utah. J. Mamm. 46: 685-687.

______. 1966. Gray fox records from western Utah. Southw. Nat. 11: 143-144.

Egoscue, H. J., and T. J. Lewis. 1968. An albino long-tailed pocket mouse from Utah. J. Mamm. 49: 319.

Fenneman, N. M. 1931. Physiography of Western United States. McGraw-Hill Book Co., New York, xiii + 534 pp.

Findley, J. S. 1969. Biogeography of southwestern boreal and desert mammals. Misc. Publ., Univ. Kansas Mus. Nat. Hist. 51: 113-128.

Findley, J. S., A. H. Harris, D. E. Wilson, and C. Jones. 1975. Mammals of New Mexico. Univ. New Mexico Press, Albuquerque, xiii + 360 pp.

Genoways, H. H., and J. K. Jones, Jr. 1967. Notes on distribution and variation in the Mexican big-eared bat, *Plecotus phyllotis*. Southw. Nat. 12: 477-480.

Hagmeier, E. S. 1966. A numerical analysis of the distributional patterns of North American mammals, II. Re-evaluation of the provinces. Syst. Zool. 15: 279-299.

Hagmeier, E. S., and C. D. Stults. 1964. A numerical analysis of the distributional patterns of North American mammals. Syst. Zool 13: 125-155.

Hall, E. R. 1946. Mammals of Nevada. Univ. California Press., Berkeley, xi + 710 pp.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Ronald Press Co., New York, 2 vols.

Hansen, R. M. 1953. Richardson ground squirrel in Utah. J. Mamm. 34: 131-132.

Harris, A. H. 1974. *Myotis yumanensis* in interior southwestern North America, with comments on *Myotis lucifugus*. J. Mamm. 55: 589-607.

Hayward, C. L., and M. L. Killpack. 1956. Occurrence of *Perognathus fasciatus* in Utah. J. Mamm. 37: 451.

______. 1958. Distribution and variation of the Utah poulation (sic) of the Great Basin pocket mouse.Great Basin Nat. 18: 26–30.

Hennings, D., and R. S. Hoffmann. in press. A review of the taxonomy of the *Sorex vagrans* species complex from western North America. Occas. Papers, Mus. Nat. Hist., Univ. Kansas.

Hultén, E. 1937. Outline of the history of the Arctic and boreal biota during the Quaternary period. Bokförlags Aktiebolaget Thule, Stockholm, 168 pp.

Jones, J. K., Jr., D. C. Carter, and H. H. Genoways. 1975. Revised checklist of North American Mammals north of Mexico. Occas. Papers Mus., Texas Tech Univ. 28: 1–14.

Keegan, H. L. 1953. Collections of parasitic mites from Utah. Great Basin Nat. 13: 35–42.

Kelson, K. R. 1951. Speciation in rodents of the Colorado River drainage. Biol. Ser., Univ. Utah. 11(3): vii + 1–125.

Kendeigh, S. C. 1954. History and evaluation of various concepts of plant and animal communities in North America. Ecology 35: 152–171.

Killpack, M. L. 1955. Notes on the thirteen-lined ground squirrel in Utah. J. Mamm. 36: 296–297.

Kottlowski, F. E., M. E. Cooley, and R. V. Ruhe. 1965. Quaternary geology of the Southwest. *In*: H. E. Wright, Jr., and D. G. Frey (eds.), Quaternary of the United States, pp. 287–298. Princeton Univ. Press, Princeton.

Krutsch, P. H., and C. A. Heppenstall. 1955. Additional distributional records of bats in Utah. J. Mamm. 36: 126–127.

Lee, M. R. 1960. Montane mammals of southeastern Utah—with emphasis on the effect of past climates upon occurrence and differentiation. Unpublished doctoral dissertation, Univ. Utah, 204 pp.

Lee, M. R., and S. D. Durrant. 1960. A new jumping mouse (*Zapus princeps* Allen) from Utah. Proc. Biol. Soc. Washington 73: 171–174.

Long, C. A. 1965. The mammals of Wyoming. Univ. Kansas Publ., Mus. Nat. Hist. 14: 493–758.

Long, C. A., and C. F. Long. 1964. Range extension of the gray fox, *Urocyon cinereoargenteus*. Southw. Nat. 9: 108–109.

Lowery, E. J., and H. J. Egoscue. 1968. The ermine in western Utah. Great Basin Nat. 28: 47.

Marshall, W. H. 1940. A survey of the mammals of the islands in Great Salt Lake, Utah. J. Mamm. 21: 144–159.

Mayr, E. 1946. History of the North American bird fauna. Wilson Bull. 58: 3–41.

Miller, A. H. 1951. An analysis of the distribution of the birds of California. Univ. California Publ. Zool. 50: 531–644.

Miller, G. S., Jr., and R. Kellogg. 1955. List of North American recent mammals. Bull. United States Nat. Mus. 205: vii + 1–954.

Morrison, R. B. 1965. Quaternary geology of the Great Basin. *In*: H. E. Wright, Jr., and D. G. Frey (eds.), Quaternary of the United States, pp. 265–285. Princeton Univ. Press, Princeton.

Musser, G. G., and S. D. Durrant. 1960. Notes on *Myotis thysanodes* in Utah. J. Mamm. 41: 393–394.

Nadler, C. R., R. S. Hoffmann, and K. R. Greer. 1971. Chromosomal divergence during evolution of ground squirrel populations (Rodentia: *Spermophilus*). Syst. Zool. 20: 298–305.

Nicholas, D. W., H. D. Smith, and M. F. Baker. 1975. Rodent populations, biomass, and community relationships in *Artemesia tridentata*, Rush Valley, Utah. Great Basin Nat., 35: 191–202.

Pizzimenti, J. J., and G. D. Collier. 1975. *Cynomys parvidens*. Mamm. Species 52: 1–3.

Poché, R. M. 1975. New record of the bat *Plecotus phyllotis* from Utah. Great Basin Nat. 35: 452.

Poché, R. M., and G. L. Baile. 1974. Notes on the spotted bat (*Euderma maculatum*) from southwest Utah. Great Basin Nat. 34: 254–256.

Poché, R. M., and G. A. Ruffner. 1975. Roosting behavior of male *Euderma maculatum* from Utah. Great Basin Nat. 35:121-122.

Polunin, N. I. 1960. Introduction to plant geography. McGraw-Hill Book Co., New York, xix + 640 pp.

Rasmussen, D. I., and N. V. Chamberlain. 1959. A new Richardson's meadow mouse from Utah. J. Mamm. 40: 53–56.

Richmond, G. M. 1965. Glaciation of the Rocky Mountains. *In*: H. E. Wright, Jr., and D. G. Frey (eds.), Quaternary of the United States, pp. 217–230. Princeton Univ. Press, Princeton.

Shippee, E. A., and H. J. Egoscue. 1958. Additional mammal records from the Bonneville Basin, Utah. J. Mamm. 39: 275–277.

Simpson, G. G. 1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. America 48: 613–687.

Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman Co., San Francisco, xiv + 359 pp.

Sparks, E. A. 1974. Checklist of Utah wild mammals. Publ., Utah Div. Wildl. Resources 74-3: x + 1–33.

Stock, A. D. 1970. Notes on mammals of southwestern Utah. J. Mamm. 51: 429–433.

Sutton, D. A., and C. F. Nadler. 1969. Chromosomes of the North American chipmunk genus *Eutamius*. J. Mamm. 50: 524–535.

Thaeler, C. S., Jr. 1972. Taxonomic status of the pocket gophers, *Thomomys idahoensis* and *Thomomys pygmaeus* (Rodentia, Geomyidae). J. Mamm. 53: 417–428.

Udvardy, M. D. F. 1969. Dynamic zoogeography with special reference to land animals. Van Nostrand, Reinhold Co., New York, xviii + 445 pp.

Wauer, R. H. 1965. Genus and species of shrew new for Utah. J. Mamm. 46: 496.

White, J. A. 1953. Taxonomy of the chipmunks, *Eutamias quadrivittatus* and *Eutamias umbrinus*. Univ. Kansas Publ., Mus. Nat. Hist. 5: 563–582.

Wood, S. L. 1958. A wolverine in Utah. Great Basin Nat. 18: 56.